Host Range, Release, and Establishment of *Sericothrips staphylinus* Haliday (Thysanoptera: Thripidae) as a Biological Control Agent for Gorse, *Ulex europaeus* L. (Fabaceae), in New Zealand and Hawaii

R. L. Hill,*,[1] G. P. Markin,†,[2] A. H. Gourlay,* S. V. Fowler,‡,[3] and E. Yoshioka§

*Landcare Research, P.O. Box 69, Lincoln, New Zealand; †USDA Forest Service, 1643 Kilauea Avenue, Hilo, Hawaii 96720;
‡CABI Bioscience, Silwood Park, Ascot SL5 7TA, United Kingdom; and §State of Hawaii Department of Agriculture,
16 East Lanikaula Street, Hilo, Hawaii 96720

This paper presents the results of tests to determine the host range of *Sericothrips staphylinus* Haliday (Thysanoptera: Thripidae), an agent selected for control of *Ulex europaeus* (Fabaceae). It also describes the biology of the thrips and its release and establishment in New Zealand and Hawaii. Eighty-three plant species were tested. Research was conducted in several institutions by use of five testing methods. Adult thrips survived for up to 15 days without food or longer on nonhost plants (causing small feeding scars). Female thrips laid eggs on several species of the Fabaceae other than *U. europaeus,* but with one exception, larvae died. *Chamaecytisus palmensis* (Christ) Bisby et K. Nichols supported the development of one adult in nine laboratory tests. Thrips produced adults on this plant in field cage tests, but in small numbers compared to controls. *S. staphylinus* appears to be narrowly oligophagous, but might establish on *C. palmensis.* At 19°C, females laid 1 egg per day on seedlings, for up to 8 weeks. Lifetime fecundity averaged 76 eggs per female. Development from egg to adult took 42 days. Thrips originating from the United Kingdom were released at 129 sites in New Zealand and have established at 59% of sites to date. Thrips originating from the United Kingdom, Portugal, and France were released in Hawaii, and all established. Thrips have caused heavy foliar damage at some field sites, and growth of the target weed has been significantly reduced in laboratory experiments. However, the impact of *S. staphylinus* on the gorse problem in New Zealand and Hawaii remains to be seen. © 2001 Academic Press

[1] Current address: Richard Hill & Associates, Private Bag 4704, Christchurch, New Zealand.
[2] Current address: USDA Forest Service, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717-0278.
[3] Current address: Landcare Research, Private Bag 92710, Auckland, New Zealand.

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INTRODUCTION

Ulex europaeus L. (Fabaceae: Genisteae) is a dense, spiny shrub that can grow to a height of over 4 m. It is native to western Europe and the British Isles, but has become naturalized in many temperate parts of the world. Gorse is a valued component of the vegetation of heathland systems in Europe but elsewhere in the world it invades disturbed or eroded habitats and has become a serious weed in pastures, forests, and undermanaged land (Hill and Sandrey, 1986). Blaschke *et al.* (1981) classified over 3.5% of New Zealand's land area as having partial or complete gorse cover. It occupies approximately 14,000 ha in Hawaii and threatens to invade even more high-altitude rangeland (Markin *et al.,* 1988; Haslewood *et al.,* 1983). It is also a land management problem in Australia, Chile, British Columbia, and the westernmost states of the continental United States. Richardson and Hill (1998) recently reviewed the biology, including the ecology, and control of *U. europaeus.*

Gorse has been the subject of considerable biological control research. *Exapion ulicis* Forster (commonly referred to as *Apion ulicis*) (Coleoptera: Apionidae) was released in New Zealand in 1931 to attack seed pods (Miller, 1970). Zwölfer (1962) and Girling (1977) reviewed opportunities for developing biological control of gorse, and a range of agents has recently been introduced into New Zealand (Harman *et al.,* 1996), to Hawaii (Markin and Yoshioka, 1996b), California and Oregon, and Chile (H. Norambuena, INIA, Carrillanca, Chile, personal communication). *Sericothrips staphylinus* Haliday (Thysanoptera: Thripidae) was among them.

The objectives of this research were (a) to examine the suitability of *S. staphylinus* as a biological control agent for gorse in New Zealand and Hawaii, (b) to describe the release and establishment of the agent in both countries, and (c) to provide an initial assessment of its likely role in the control of gorse. This paper presents the results of research into the biology, including the ecology and host range, of the thrips conducted by CABI Bioscience in the United Kingdom from 1987 to 1989 and in separate but parallel studies in New Zealand and Hawaii.

S. staphylinus Haliday 1836 belongs to the tribe Sericothripini of the family Thripidae. Jacot-Guillarmod (1971) listed 99 species in the genus, but only 4 of these species occur in Europe (3 in England). The taxonomy of the species has been revised several times. Priesner (1928) listed three forms of *S. staphylinus:* the typical form, var. *bicornis,* and var. *gracilicornis.* Others have treated these forms as distinct species (Kloet and Hincks, 1964; Morison, 1948; Jacot-Guillarmod, 1971). Bhatti (1973) revised the genus *Sericothrips* extensively, retaining *S. staphylinus* and *S. abnormis* (Karny) (=*bicornis*) but moving var. *gracilicornis* to the genus *Neohydatothrips* as *N. gracilicornis* (Williams). Through all of these revisions, the "typical" brachypterous form of *S. staphylinus* has remained recognizable as a distinct species (Bhatti, 1973).

The records of host plants for *S. staphylinus* that are available in the literature appear inconsistent. Priesner (1928, 1964) recorded *S. staphylinus* as living only on *U. europaeus* and *U. nanus* Forster. However, Jacot-Guillarmod (1971) listed a range of hosts: "*Ulex europaea* (sic); *Ulex nanus; Galium;* grass; *Vicia cracca; Lotus corniculatus;* perhaps some other leguminosae." He did not indicate whether reproduction occurred on these hosts, or whether specimens were collected as itinerant individuals. Dyadechko (1964) ascribed *S. staphylinus* pest status on inflorescences of fruit and berry plants. This interpretation appears to result from an uncritical application of the collective host ranges of Priesner's (1928) forms of the species (particularly *N. gracilicornis,* which feeds in rosaceous flowers) to each of the revised species. *S. staphylinus* has been reliably recorded on plants other than *U. europaeus* on occasions in Britain, but is generally considered to be monophagous on this host (Dr. J. Palmer, British Museum, Natural History, London, personal communication).

A number of taxa assigned to the genus *Sericothrips* have been recorded as pests of crops worldwide. However, when Bhatti (1973) revised the genus *Sericothrips,* most were reassigned to genera other than *Sericothrips.* These included *Hydatothrips adolfifriderici* Karny (=*S. occipitalis* Hood) on cowpeas in Africa, *Neohydatothrips variabilis* (Beach) (=*S. variabilis*) on soybeans in the United States, *N. inversus* (Hood) (=*S. inversus*) on cacao in the Carribbean, and *N. gracilicornis* (=*S. gracilicornis* Williams) on rosaceous flowers in eastern Europe (see also Nakahara, 1988). Original names are sometimes still used in the literature (e.g., Huckaba and Coble, 1990). The *Sericothrips* species recorded in Europe feed mostly on legumes.

MATERIALS AND METHODS

Insect Collection and Rearing

Populations of *S. staphylinus* used in this research came from three sources: (i) Yateley Common, Hampshire, United Kingdom; (ii) São Pedro de Muel, Portugal; and (iii) Nantes, France. Thrips obtained from Portugal and France interbred freely with those of English origin, and there appeared to be no reproductive isolation. All host-range tests reported in this paper were conducted using English thrips only. However, in a small series of tests not reported here, a limited number of critical host plants were exposed to thrips from the other two populations by use of the same methods. The results of these tests were the same for all populations (G. P. Markin, unpublished data). For these reasons, host-range test results presented here were assumed to apply to thrips from all three sources. Thrips released in New Zealand originated from Yateley Common, United Kingdom, and thrips from all three source populations were released in Hawaii.

Experiments conducted in the United Kingdom used thrips collected locally at Yateley Common. In New Zealand, adults were drawn from a continuous colony originating from the same source but maintained in a secure containment facility on potted *U. europaeus* plants held in fine-cloth cages. In Hawaii, colonies of all three populations were established on 15-cm-tall potted seedlings held in wide-mouthed gallon jars. Ten unsexed newly emerged adults were placed on each bouquet and the jar mouth was covered with organdy cloth secured by a rubber band. After 49 days the colony contained approximately 50 new adults and nymphs at various stages of development. Two colonies were established each week, and newly imported thrips were incorporated into the colonies in 1988 and 1989.

Biology

The longevity and fecundity of adult thrips were measured under laboratory conditions in New Zealand. Thrips could not be sexed reliably, so teneral thrips were paired by selecting one large and one small thrips. Single pairs were transferred using a camel-hair brush to 3-cm-tall *U. europaeus* seedlings growing in 8-cm-diameter pots. Pots were then placed in 1-cm-deep water and covered with 30-cm-tall, 15-cm-diameter, ventilated clear plastic cylinders to prevent the

thrips' migration to or from seedlings. Plants were randomly assigned on a bench in a strongly lit room at an average temperature of 19°C (mean diurnal range 16.4–22.2°C) and a 16:8 h light:dark regime. Plants were examined every 2–3 days, and the presence of adults was recorded. Longevity was estimated as the period over which adults could be found. Original adults were transferred to a new seedling before the development of offspring was completed. Lifetime fecundity was estimated as the maximum number of offspring recorded on all plants used by the parent female. Daily oviposition rate was calculated.

The time for each immature stage to develop at 19°C was measured as follows. Approximately 30 adult thrips were collected from a gorse bush in the laboratory and transferred to two 3-cm-tall, thrips-free seedlings to lay eggs. Thrips were removed 24 h later. This was repeated on 3 separate days to produce four cohorts of eggs that were up to 1 day old. The eight uncovered pots were randomly arranged on a bench. Seedlings were examined every 2–4 days, and the number of thrips in each developmental stage was recorded. The date at which 20–50% of thrips had moved from one developmental stage to the next was estimated. The development time for each stage was calculated and averaged across the eight plants. Biological and developmental characteristics of *S. staphylinus* were observed and recorded in the course of the rearing of insects for experimentation in the United Kingdom and Hawaii.

Host-Range Tests

Selection of test plants. The ability of adult thrips to survive and oviposit and that of larvae to complete development on plants other than *Ulex* species were determined experimentally. The selection of test plants broadly followed the principles outlined by Wapshere (1975). Plants tested in the United Kingdom and New Zealand were selected largely from the Fabaceae, concentrating on species closely related to gorse within the tribe Genisteae. At least 17 species of the New Zealand endemic genus *Carmichaelia* (Heenan, 1998), *Clianthus puniceus* (G. Don) Sol. ex Lindl., and 3 native species of the genus *Sophora* were tested. A representative selection of species belonging to other fabaceous tribes was tested, with emphasis on species of economic importance. Finally, a range of species belonging to other plant families in New Zealand was tested. Subsequent host-range tests in Hawaii included representatives of native and economically important legumes, but with the exception of particular Hawaiian varieties of some species, these did not duplicate previous research. In addition, 25 species representing 15 diverse families of economically important crops, ornamentals, or native forest plants found in Hawaii were tested.

Test methods. Laboratory tests in the United Kingdom were conducted under ambient laboratory conditions in summer at CABI Bioscience, Silwood Park. Laboratory tests were carried out in New Zealand during 1989 in a secure containment facility at Lincoln, Canterbury, at a 20:12°C, 16:8 h light:dark regime at approximately 75% relative humidity. Tests in Hawaii were conducted at the US Department of the Interior's Insect Quarantine Facility located in a temperate climate at 1140 m altitude in the Hawaii Volcanoes National Park. The facility was maintained at ambient temperature and humidity.

For test method 1, 10-cm lengths of test plant stems were prepared. The cut end of the stem was inserted through a waterproof stopper into a vial containing water. An insect-resistant cylindrical plastic cover was placed over the shoot to minimize insect migration, and five unsexed adult thrips were confined on the shoots. Feeding intensity and survival of adults on test plants was determined after 1 to 4 weeks, and the number of adults and larvae present was recorded. In the United Kingdom in 1987, each test was stopped after 3 weeks, and the number of frass spots present was also estimated. In Hawaii, some tests were also conducted by the placing of foliage on damp filter paper in a petri dish followed by the introduction of the thrips. Shoots were changed weekly. Samples were examined weekly to determine the numbers of surviving adult thrips and feeding scars and the presence of frass particles; each test was replicated three to five times. In all tests, plant material appeared to remain in good condition for approximately 3 weeks, but not long enough to adequately measure larval survival (approx. 6 weeks).

For test method 2, cylindrical or conical plastic or glass covers sealed at the top with fine cloth were placed over small plants growing in pots. Ten unsexed thrips were added to each plant and the plants were checked for the presence of new-generation thrips after 7 weeks. Alternatively, 2-cm-diameter, 1-cm-tall, close-fitting, open-bottomed cages made of plastic were clipped to the leaf surface of growing plants, and 10 unsexed thrips were added. The number of adults and larvae present after 2 weeks was recorded, and after 7 weeks the cages were checked for the presence of new-generation thrips. The clip-cage method was not used extensively.

Adult thrips were able to survive for a significant period on cut shoots of a limited number of the plant species in laboratory tests. This ability was examined more closely by observation of survival and reproduction on growing plants in larger cages. For test method 3, a series of potted test plants were placed in cloth cages (1 × 1 × 1 m). Stems of potted plants of *Sophora microphylla* Aiton and *C. puniceus* (G. Don) Solander ex Lindley that were too large for the cage were introduced through the sides. Five *Sericothrips* adults were introduced to the base of each plant or stem. After 3

weeks, a sample of the foliage from each test plant was placed in a plastic bag and shaken to remove all insects. Thrips were removed and identified. A sample was also taken from gorse foliage. The number of adult *S. staphylinus* on various species was recorded (Howard, 1989).

For test method 4, a selection of potted plants was placed on metal frames adjacent to gorse bushes in the field at Yateley Common, Hampshire, United Kingdom and arranged so that foliage touched gorse plants naturally infested with *S. staphylinus.* After 1 month, a sample of the foliage from each test plant was placed in a plastic bag and shaken to remove all insects. Thrips were removed and identified. The number of adults, prepupae, pupae, and larvae of gorse thrips was recorded. Nine days later, thrips were extracted from the remaining test foliage in the same way (Howard, 1989).

For test method 5, choice tests in quarantine in Hawaii were conducted by placing 25- to 45-cm-tall potted test plants and a similar-sized potted gorse plant in a glass-topped sleeve cage (0.4 × 0.45 × 0.53 m). Approximately 50 adult thrips were added and allowed to choose between plants for 7–14 weeks. This population density was used because similar populations were known to stress and sometimes kill small gorse plants, forcing migration of the thrips to adjacent plants. The feeding damage and presence of nymphs on each plant was recorded after 7 weeks. Tests were replicated once for each plant species.

Release and Establishment

Permission to release *S. staphylinus* in New Zealand was granted in August 1990, and laboratory cultures were established on potted plants in the laboratory. Once populations had grown, adults were collected for field release by the beating of foliage of these plants over a white surface and the aspiration of the thrips that fell. Thrips were released onto 15-cm-long bouquets of gorse foliage with stems usually packed in wet cotton wool, and these were packed into plastic boxes for despatch and release. Sites were selected throughout New Zealand, and thrips were released within 48 h of collection from the laboratory. An isolated bush was selected at each release site, and thrips were transferred by lodging the bouquet in the bush. An isolated bush was chosen to minimize thrips migration while populations established. Population establishment was monitored at most sites by observation of adults on foliage and by the beating of foliage to dislodge the thrips onto a white cloth. A population was judged to have established if it appeared to have increased in successive years. No formal population measurements were made.

On the island of Hawaii, thrips were released at 13 widely spaced sites in a semicontinuous gorse infestation growing at approximately 1830 m altitude at Hu-

mu'ula, 45 km from Hilo on Highway 20. Releases were made along a road running the 10-km length of the core infestation, which is 1–2 km wide (Markin and Yoshioka, 1996a). A variety of release methods were employed, including cages, bags, and free release, and releases were repeated many times at each site. Thrips from a single-source population were released at some sites, but two or three strains were released at others. Two sites were enclosed with fences to exclude cattle, and these sites were used to monitor the establishment of thrips of English and Portuguese origin. Thrips beaten from one 40-cm branch on each of 10 plants growing within 1–3 m were counted. Once populations were large enough to harvest, whole infested plants were collected into bags near release points and deposited in gorse plants at 64 new sites within the mostly densely infested area of gorse. Once common throughout the area, thrips of different origins could not be distinguished in the field.

Thrips originating from England (three releases totaling 850 thrips) and Portugal (two releases totaling 300 thrips) have also been released near Olinda (800–1000 m a.s.l.) and near Haleakala National Park (1800–2000 m a.s.l.) on the Hawaiian island of Maui, but details of these releases are not known.

RESULTS

Biology

S. staphylinus is a short, robust thrips that appears black except for distinctive white rudimentary wing pads and a layer of shiny adpressed hairs on the abdomen. Although normally brachypterous, winged adults occurred occasionally and were found throughout the year. Brachypterous adults were mobile and able to jump 5 cm or more. Females were longer (1.02–1.17 mm) than males (0.74–0.87 mm). In females, the abdomen was slightly wider than the thorax, but the males were more slender.

There was an 8- to 12-day preoviposition period. Eggs were produced singly, were white to pale yellow, were slightly curved with a tapered cylindrical shape, and were approximately 0.3 mm long. The eggs were laid in slits in the young stems of the host plant and protruded slightly. In New Zealand studies, mean (±SE) lifetime fecundity was 76.2 ± 8.9 (n = 20). At 19°C, females laid at a rate of 2.0 ± 0.13 eggs/day (n = 24), and the life span of ovipositing adults was 32.5 ± 4.1 days. In Hawaii, at similar temperatures, the oviposition rate recorded was only 0.2–0.5 eggs per day, and each female produced 7–14 eggs (max 20) over an 8-week life span. The reasons for these large differences in performance are uncertain, but Hawaiian studies were conducted on older plants, and the differences may be due to relative food quality.

At 19°C, eggs hatched after 20 days (range for eight plants was 17–23 days). First-stage larvae were delicate and cream-colored, and they molted within 2–4 days. Second-stage larvae were yellow and robust, with pigmented eyes. The combined larval period was 13.1 days (range 11–16 days). Prepupae had short antennae with obscure segmentation, small eyes, a paler body with a smoother cuticle, and fewer, but longer, hairs than the larvae. Antennae were short and projected forward. The prepupae remained mobile but did not feed. Prepupal period was 3.2 days (range 2–6 days). The long antennae of pupae were recurved over the prothorax, and this distinguished pupae from prepupae. Both were found on gorse shoots in laboratory cultures, and it appears unlikely that the larvae move onto leaf litter, moss, etc. to pupate in the field as reported for some other Thripidae (Ananthakrishnan, 1984). The mean development time from eggs to adult at 19°C was 42.0 days (range 35–49 days).

Both adults and larvae of *S. staphylinus* fed on the mesophyll of *Ulex* spp., and at high densities removal of the mesophyll layer produced pale, stippled areas on gorse leaves, spines, and stems. Black frass droplets were produced copiously and provided one method for assessing the extent of feeding by thrips on plants in host-range tests. Thrips of all stages could feed successfully on all green foliage, but avoided actively growing shoot tips. The adults overwintered on gorse foliage, presumably living for at least 10 months, and could be collected throughout the year. Adults collected from the field in the United Kingdom in December or January, and placed on growing gorse plants at room temperature, produced larvae within 20 days. In the field, larvae were collected from May until late September in the United Kingdom, but with a clear peak in numbers in June and July/August. It appears that *S. staphylinus* can be multivoltine but that the number of thrips produced in subsequent generations in a given year is very much smaller than that in the first generation, perhaps because of the poor nutritional quality of gorse foliage for most of the year (Hill, 1982).

Host-Range Tests

Testing methods varied between laboratories, and results were sometimes recorded differently (Table 1), but the pattern of host-range utilization revealed was consistent.

Tests on cut shoots. In tests conducted in Hawaii adult *S. staphylinus* were confined on cut shoots of 25 forest and agriculturally important plant species. Thrips survived best on *U. europaeus* (Table 1), but a significant proportion persisted for long periods, even on plants only remotely related to the true host. Other than on legumes, occasional lesions (attributed to exploratory feeding) could be detected on about half of the plant species presented (Table 1). Thrips caused little visible damage to those plants and produced few frass droplets compared to controls. Most died within 1 week, although some (including those confined on *Sophora chrysophylla* (Salisb.) Seem and *Medicago sativa* L.) survived for over 4 weeks. Adults survived for 15 days in petri dishes with damp filter paper alone, suggesting that adults can live for a long time without feeding. In one set of tests, control shoots of *U. europaeus* were destroyed by thrips in 4–5 weeks, but adults remained on test-plant shoots for 10 weeks without causing visible damage.

Results obtained in New Zealand and United Kingdom were similar to those obtained in Hawaii (Table 1). Thrips usually attempted exploratory feeding on test plants. Some adults survived for more than 3 weeks, and a few lived as long as 7 weeks. This range was comparable to survival on the gorse controls. *S. staphylinus* laid eggs on cut shoots of several test plants, but more larvae hatched on *U. europaeus* than on other species. This may be because adults placed on *U. europaeus* survived longer and so had greater opportunity to lay eggs or because gorse was more acceptable as a host. No larvae were found on 24 of the 37 fabaceous species tested. Larvae hatched on cut shoots of eight test plants, but the number ranged from 0.5–3.0% of the number recorded hatching on gorse. It is possible that some of the thrips recorded were larvae of other species hatching from eggs laid before the stem was exposed to *S. staphylinus.* Larvae could not be reared for identification. Significant numbers of thrips larvae were recorded on shoots of *M. sativa, Phaseolus vulgaris L., S. chrysophylla, Trifolium repens L.,* and *Vicia sativa L.,* but the shoots died before the ability of these larvae to develop could be assessed.

Tests on whole plants. Thrips were confined on growing plants using clip-cages or sleeves to determine whether *S. staphylinus* could lay eggs and then complete development on test-plant species (test method 2). More adults were recorded on gorse than on test plants during this experiment (Table 1). Thrips were difficult to contain, and the loss of thrips from experiments was a combination of mortality and emigration. Few thrips emigrated from controls, and since emigration indicates dissatisfaction with the test plant, this loss was regarded as an indicator of host plant suitability. First-stage larvae were recorded on five legume species but in small numbers in comparison to controls (Table 1). Larvae were observed on *Lupinus arboreus* Sims, *M. sativa,* and *S. chrysophylla* but did not grow and died within 1 week. In three replicates, a total of five larvae hatched on *Chamaecytisus palmensis* (Christ) Bisby et K. Nicholls. One adult was produced, the only plant species other than *U. europaeus* on which *S. staphylinus* completed development.

Further tests were conducted on whole plants. Approximately 50% of thrips remained on nine test spe-

TABLE 1

Oviposition and Survival of *Sericothrips staphylinus* on Nontarget Plants as Revealed by
Host-Range Tests (Methods 1 and 2)

Species	FAMILY Tribe	No. of tests	Mean No. after 4 or 7* weeks — Adults	Larvae	Age of oldest adult (days)	Feeding index[a]	Frass drops/ adult/ day	Control No.[b]	Site of tests	No. of tests	Control No.[b]	Feeding index[a]	Mean No. at 3‡, 6†, or 8 weeks — Larvae	Adults	Site of tests
	FABACEAE														
Ulex europaeus L.	Genisteae							1	UK	5	11		23.6†		UK
U. europaeus		15	1.9	20.9 ± 6.3	d			2	UK	4	12		17‡	>1	UK
U. europaeus		4	3.0*	34.0*				3	NZ	3	13	*****	55	17	HI
U. europaeus		4	3.3*	33.8*				4	NZ	3	14	*****	143	118	HI
U. europaeus		3			30+	****	5–6	5	HI	3	15	****	131	128	HI
U. europaeus		6			30+	****	6–7	6	HI	3	16	****	64	53	HI
U. europaeus		3			70+	*****	6–7	7	HI	3	17	****	80	79	HI
U. europaeus		3			43	*****	6	8	HI	3	18	****	189	210	HI
U. europaeus		3			53	*****	5–6	9	HI	3	19		16.3†	9.0†	NZ
U. europaeus		3			60+	*****	6–8	10	HI	3	20		33.3†	9.7†	NZ
										3	21		23.0†	3.0†	NZ
Colutea arborescens L.		10	0.1 ± 0.1	0.1 ± 0.1				2	UK						
Chamaecytisus palmensis (Christ) Bisby et K. Nicholls		6	0	0.2 ± 0.2				2	UK	3	11		0†	—d	UK
										2	12		0‡	0	UK
										3	15–20	***	5	1	HI
Cytisus scoparius L. (Link)		3			27	**	1–2	5–10	HI	5	11		0†	—	UK
		5	0	0				2	UK	3	15–20	**	2	0	HI
Genista hispanica L.		8	0.6 ± 0.5	0.13				2	UK	4	11		0†	—	UK
										3	12		0‡	0	UK
G. tinctoria L.		6	2.2 ± 0.5	2.2				2	UK	4	11		0†	—	UK
										4	12		0‡	0	UK
Laburnum anagyroides Medikus		1	0	0				2	UK						
Lupinus angustifolius L.										3	15–20	0	0	0	HI
L. arboreus Sims		3			35	*	<1	5–10	HI	3	15–20	**	1^c	0	HI
		3	0.3 ± 0.3	0				2	UK						
Lupinus sp.		7	1.3 ± 0.3	0.4 ± 0.3				2	UK	4	11		0†	—	UK
										3	12		0‡	—	UK
Spartium junceum L.		5	1.6 ± 0.6	3.2 ± 3.2				2	UK	4	12		0‡	—	UK
Carmichaelia aligera Simpson	Carmichaeliae	4	0*	0*				4	NZ						
C. arborea (Forst. f.) Druce		2	2.0 ± 2.0	0				2	UK	4	11		0†	—	UK
C. compacta Petrie		4	2.0 ± 0.9	0				2	UK	3	11		0†	—	UK
C. corrugata Col.		3	0.3	0				3	NZ						
C. enysii Kirk		3	2.0*	0*				3	NZ						
C. exsul F. Muell.		4	0*	0*				4	NZ						
C. glabrescens (Petrie) Heenan		7	0.4 ± 0.3	0				2	UK						
C. kirkii Hook. f.		4	0*	0*				3	NZ						
C. monroi Hook. f.		2	0	0				2	UK						
C. muritai (A. W. Purdie) Heenan		4	0*	0*				3	NZ						
C. odorata Col. Ex Hook. f.		4	0*	0*				4	NZ						
C. petriei Kirk		4	1.0*	0*				3	NZ						
C. ramosa Simpson										4	11		0†	—	UK
C. stevensonii (Cheeseman) Heenan		5	0.2 ± 0.2	0				2	UK	4	11		0†	—	UK
C. torulosa (Kirk) Heenan		3	0	0				3	NZ						
C. williamsii Kirk		3	0.3*	0*				4	NZ						
Acacia koa Gray	Acacieae	5	0	0				2	UK	3	12		0‡	0	UK
										3	15–20	*	0	0	HI
A. koaia Hbd.										3	15–20	*	0	0	HI
A. melanoxylon R. Br.										3	19		0†	0†	NZ
Desmodium sp.	Desmodieae	3			25	0	<1	5–10	HI						
Clianthus puniceus (G. Don) Sol. ex Lindl.	Galegeae									2	12		2.5‡	0	UK
										3	19		0†	0†	NZ
Prosopis pallida (Humboldt & Bonpland ex Willdenow) Kunth	Mimoseae	3			42	*	<1	5–10	HI	3	15–20	*	0	0	HI
Sophora chrysophylla (Salisb.) Seem	Sophoreae	3			64	**	<1	5–10	HI	2	12		0‡	0	UK
		6	1.0 ± 0.5	1.0 ± 0.6				2	UK	3	15–20	**	2^c	0	HI
S. microphylla Aiton		10	0	0.1 ± 0.1				2	UK	2	12		0‡	0	UK
										3	21		0†	0†	NZ
S. prostrata Buchan.		4	0*	0*				3	NZ						

TABLE 1—*Continued*

Species	FAMILY Tribe	Test method 1 adult survival and oviposition on cut shoots								Test method 2 oviposition and larval development					
		No. of tests	Mean No. after 4 or 7* weeks		Age of oldest adult (days)	Feeding index[a]	Frass drops/ adult/ day	Control No.[b]	Site of tests	No. of tests	Control No.[b]	Feeding index[a]	Mean No. at 3‡, 6†, or 8 weeks		Site of tests
			Adults	Larvae									Larvae	Adults	
Wisteria sinensis (Sims) Sweet	Tephrosieae	3	0.7 ± 0.7	0.3 ± 0.3				2	UK						
Lotus corniculatus L.	Trifolieae	11	2.3	4.2				2	UK	3	15–20	**	0	0	HI
L. pedunculatus Cav.										3	19		0†	0†	NZ
Medicago sativa L.		10	2.4 ± 0.5	4.6 ± 2.2				2	UK	2	11		0†	—	UK
		3			84	**	1–2	5–10	HI	3	15–20	***	2[c]	0	HI
										3	19		0†	0†	NZ
Trifolium ambiguum M. Bieb.		3	1.7 ± 1.2	0				2	UK	1	12		0‡	0	UK
T. hybridum L.		1	0	0				2	UK						
T. pratense L.										3	15–20	*	0	0	HI
										2	19		0†	0†	NZ
T. repens L.		10	2.9 ± 0.5	0.5 ± 0.3				2	UK	3	15–20	**	0	0	HI
		3			43	***	2–3	5–10	HI	3	19		0†	0†	NZ
Trifolium sp.										3	11		0†	—	UK
Glycine max (L.) Merrill	Vicieae									2	12		0‡	0	UK
										3	15–20	**	0	0	HI
										3	15–20	**	0	0	HI
										2	20		0†	0†	NZ
Lens culinaris Medikus										3	19		0†	0†	NZ
Phaseolus vulgaris L.		4	0	0.5 ± 0.3				2	UK	2	12		0‡	0	UK
										3	15–20	*	0	0	HI
										2	20		0†	0†	NZ
Pisum sativum L.		4	0	0.3 ± 0.3				2	UK	2	12		0*	0	UK
										3	15–20	*	0	0	HI
										3	21		0†	0†	NZ
Vicia faba L.		4	0.5 ± 0.5	0.3 ± 0.3				2	UK	1	12		0‡	—	UK
										3	19		0†	0†	NZ
V. menziesii Spreng.		6			28	**	1–3	5–10	HI						
V. sativa L.		5	0.2 ± 0.2	0.6 ± 0.4				2	UK	3	15–20	*	0	0	HI
Erythrina sandwicensis Gray										3	15–20	**	0	0	HI
Actinidia sp.	ACTINIDIACEAE	3	0	0				2	UK						
Alyxia olivaeformis Gaud.	APOCYNACEAE	6			45	*	0	5–10	HI						
Anthurium andreanum Lind.	ARACEAE	3			17	0	0	5–10	HI						
Dubautia arborea (Gray)	ASTERACEAE	3			33	*	<1	5–10	HI						
Lactuca sativa L.		6			24	0	0	5–10	HI						
Olearia haastii Hook. f.		5	0.6 ± 0.6	0				2	UK	5	11		0†	—	UK
Brassica sp.	BRASSICACEAE	6			20	*	0	5–10	HI						
Ananas comosus (Stickm.) Herr.	BROMELIACEAE	3			12	0	0	5–10	HI						
Carica papaya L.	CARICACEAE	3			18	*	0	5–10	HI						
Cibotium chamissoi Kaulf.	DICKSONIACEAE	3			28	0	0	5–10	HI						
Vaccinium reticulatum Sm.	ERICACEAE	6			32	*	0	5–10	HI						
Pennisetum clandestinum Chiov.	GRAMINEAE	3			15	*	<1	5–10	HI						
Saccharum officinarum L.		3			21	*	0	5–10	HI						
Heliconia sp.	MUSACEAE	3			62	*	<1	5–10	HI						
Myrica faya Aiton	MYRICACEAE	3			15	*	<1	5–10	HI						
Eucalyptus sp.	MYRTACEAE	5	0	0				2	UK						
Metrosideros collina (J. R. & G. Forst.) Gray		6			45	*	0	5–10	HI						
Psidium guajava L.		6			36	0	0	5–10	HI						
Phalaenopsis sp.	ORCHIDACEAE	6			13	0	0	5–10	HI						
Pinus sylvestris L.	PINACEAE	5	0	0			0	2	UK						
Macadamia integrifolia Maiden & Betche	PROTEACEAE	6			7	0	—	5–10	HI						
Rosa sp.	ROSACEAE	3			57	*	<1	5–10	HI						
Rubus hawaiiensis Gray		4			14	0	0	5–10	HI						
Coffea arabica L.	RUBIACEAE	3			11	0	0	5–10	HI						
Hebe rakaiensis (J. B. Armst.) Ckn.	SCROPHULARIACEAE									3	11		0†	—	UK
Ipomoea batatas (L.) Lam.	SOLANACEAE	2	0	0				2	UK						
Pipturus albidus (H & A) Gray	URTICACEAE	3			12	0	0	5–10	HI						
Viola serpens Wall.	VIOLACEAE	3			24	*	<1	5–10	HI						
Hedychium coronarium Koenig in Retz.	ZINGIBERACEAE	3			24	*	<1	5–10	HI						
Zingiber officinale Roscoe		3			17	*	<1	5–10	HI						

[a] 0, no feeding; *, exploratory feeding; **, light feeding; ***, moderate feeding; ****, heavy feeding; *****, very heavy feeding.

[b] The control data associated with each set of results.

[c] Larvae died within 1 week.

[d] A dash or a gap indicates that there are no data.

TABLE 2

Presence of *Sericothrips staphylinus* on Test Plants after Field Exposure to Thrips at
Yateley Common, United Kingdom (Method 4)

Species	Tribe	No. of tests	Mean number after 4 weeks		Mean number after 6 weeks	
			Larvae	Adults	Larvae	Adults
Ulex europaeus L.	Genisteae	3	7	7	15	24
Carmichaelia sp. 1	Carmichaeliae	1	0	0	0	0
Carmichaelia sp. 2		2	0	0	0	0
Lupinus sp.	Genisteae	3	0	0.3	0.3	0.3
Lotus corniculatus L.	Trifolieae	3	1.3	0	0.3	0
Medicago sativa L.		3	0	0.3	0.6	1
Trifolium pratense L.		3	0	0	0	1

cies after 3–4 weeks. These plants included *Trifolium* species, *M. sativa, Carmichaelia* species, *Lotus corniculatus* L., and several species closely related to *U. europaeus* within the tribe Genisteae.

Three tests were conducted in which thrips were able to choose to colonize *U. europaeus* or test plants. We selected test plants on which larvae had been recorded in no-choice tests. After 2 months in the field test (test method 4, Table 2), at least 20 times more thrips were found on *U. europaeus* plants than on any test plant, and three of the six test plants had no thrips at all. In tests conducted in cages in the United Kingdom, *S. staphylinus* adults migrated to *U. europaeus* plants, and few were found on test plant foliage after 5 weeks (Table 3). One immature stage was found on *L. corniculatus,* but this may have wandered from *U. europaeus.* In a robust experiment conducted in Hawaii, plants were exposed to high initial populations of thrips. After 7–12 weeks, all control plants were either dead or dying because of thrips damage (Table 4). *P. vulgaris* plants tested also died, but there was no evidence of feeding damage from thrips. Similarly, there was no evidence of feeding damage on *Acacia koa, S. chrysophylla,* or *T. repens.* On *L. arboreus* and *L. angustifolius* L., there were no thrips present at the end of the experiment; plants were healthy, but feeding scars were evident. After 8 weeks, there had been some light feeding on *Cytisus scoparius* L. (Link), but no thrips were present at the end of the test. Thrips were abundant on the control, and feeding damage was heavy. Similarly, *C. palmensis* plants sustained light feeding damage throughout the tests, but 10 adults were present at the conclusion of the test. The test was terminated because control plants in the cage were dying from attack by abundant thrips.

Release and Establishment

S. staphylinus was released at 210 sites throughout New Zealand from October 1990 until June 1998 (Fig. 1). Thrips have established at 80% of the 44 release sites at which the fate of the thrips is known. The remainder have not been revisited, or releases have been too recent to assess. The thrips has established in all regions of New Zealand (Fig. 1), and

TABLE 3

Presence of *Sericothrips staphylinus* on Test Plants Infested with Five Adults in Four Cages (Method 3)[a]

Species	Tribe	No. of tests	Mean No. per plant		
			Adults, 2 weeks	Immatures, 5 weeks	Adults, 5 weeks
Ulex europaeus L.	Genisteae	7	2.4	44.7	4.3
Carmichaelia sp.	Carmichaeliae	4	0	0	0
Clianthus puniceus (G. Don) ex Sol. et Lindl.	Galegeae	1	0	0	0
Lupinus sp. (Russell)	Genisteae	3	0	0	0
Spartium junceum L.		4	0	0	0.3
Sophora microphylla Aiton	Sophoreae	1	0	0	0
Lotus corniculatus L.	Trifolieae	7	0.1	0.1	0
Medicago sp.		4	0	0	0
Trifolium pratense L.		4	0	0	0.3

[a] Tests were conducted in the United Kingdom.

TABLE 4

Performance of *Sericothrips staphylinus* on Potted Test Plants Housed in Small Laboratory Cages
with Potted *Ulex europaeus* Plants in Hawaii[a]

Test plant	Test ended after (days)	Final observations on gorse	Final observations on test plant
Acacia koa Gray	50	Heavy feeding; plant dying; high thrips population	No feeding; no thrips observed
Chamaecytisus palmensis (Christ) Bisby et K. Nicholls	60	Heavy feeding; gorse dying; strong population of thrips	Light feeding; 10 adults present; thrips observed rarely during test.
Cytisus scoparius (L.) Link	110	Heavy feeding; adults and nymphs abundant	Light damage; no adults present; adults observed feeding throughout
Lupinus angustifolius L.	100	Plant killed by thrips feeding	Plant healthy; no thrips found; exploratory feeding observed during test
Lupinus arboreus Sims	110	Plant killed by thrips feeding	No feeding damage; no thrips; several thrips observed in midtest
Phaseolus vulgaris L.	80	Heavy feeding; thrips abundant	Plants dead from confinement; no feeding observed; no thrips present
Sophora chrysophylla (Salisb) Seem	50	Plant dead; 300+ thrips dead in cage	No feeding; no thrips present
Trifolium repens L.	60	Plant dying; heavy feeding observed	No feeding; no thrips; several thrips observed early

[a] Each test was repeated once.

there is no discernible pattern to establishment success. Dispersal has been slow. At the original release site, thrips have moved up to 500 m altitude, population numbers are high, and visible damage to bushes near the release point has been observed (J. Sheat, Landcare Research, New Zealand, personal communication). However, at most sites, thrips have moved no more than 10–20 m per year, and bronzing is restricted to the bushes on which the releases were made.

In Hawaii, *S. staphylinus* was first released at Mauna Kea in May 1991, and there were multiple releases at the selected sites for 24 months (Table 5). At site 3, thrips of English origin were released in May 1991. Three years later, the density of thrips at the release point was 10–15 thrips per branch, but no thrips could be detected 50 m away from the release point. At site 9, thrips of Portuguese origin had reached a density of 5 thrips per branch at the release point after 18 months and could be detected 25 m from the release point. After 30 months, thrips could be found 250 m away and had achieved a density of 20 per branch at the release point. Six years after the first release, and 3 years after the thrips were redistributed, populations could be detected uniformly at 28 of 32 sites that were randomly selected within the core infestation. However, mean density of populations did not exceed 1 thrips per branch. Nothing is known about the relative contribution to the population of thrips of different origin.

FIG. 1. Sites in New Zealand at which *Sericothrips staphylinus* has been released and is known to be established. The status of many sites is not known, and some releases are too recent to judge establishment (○, release points; ●, known establishments; some symbols represent more than one site).

TABLE 5

The Number of *Sericothrips staphylinus* Released at
Mauna Kea, Hawaii between May 1991 and April 1993[a]

	Founding population originating from		
Site	United Kingdom	Portugal	France
1	1250	1225	1150
2	1350	0	0
3	2285	0	0
4	640	0	0
5	675	0	0
6	2345	0	0
7	350	0	0
8	100	995	0
9	0	2080	0
10	0	850	0
11	0	2690	0
12	0	0	2180
13	0	0	700
Thrips released	8995	7840	4030
Number of releases	50	31	22

[a] Sites are listed south to north along the Contour Road arising from Highway 20 at Humu'ula.

DISCUSSION

S. staphylinus is commonly found on *Ulex* spp. in the United Kingdom and continental Europe (Zwölfer, 1962; Hill, 1982; O'Donnell, 1986). It has been recorded from other host plants, but as outlined in the Introduction, the value of these records must be questioned, and there are no reliable records of it reproducing on other plant species. Host-range experiments also demonstrate that, with the possible exception of *C. palmensis,* *S. staphylinus* cannot reproduce on plants other than *Ulex* species. Tests employed in this study ranged from no-choice tests using cut shoots to field experiments and occurred under different conditions in three countries. In all, 83 plant species were tested. Female thrips laid occasional eggs on 12 leguminous plant species in tests, mostly those within the same tribe as *Ulex* spp. Hatching larvae survived poorly on plants other than *Ulex* spp., and only *C. palmensis* supported full development, a single individual developing from egg to adult over six tests. In general, these tests strongly indicate that *S. staphylinus* is a narrowly oligophagous species, which can be expected to develop significant populations only on *Ulex* spp. in the field.

It proved difficult to contain thrips within test arenas, and it is possible that some of the results obtained were from experimental contamination rather than due to positive host selection. If so, the potential host range revealed by these data may be overstated. *C. palmensis* supported complete development of a single *S. staphylinus* in laboratory tests and could be regarded as a potential alternative host for the thrips in New Zealand. However, monitoring of *C. palmensis*

plants growing near thrips-infested gorse in New Zealand has revealed no evidence of colonization (A. H. Gourlay, Landcare Research, personal communication). Thrips laid eggs that produced larvae relatively freely on alfalfa, *M. sativa,* but none completed development. Other agents developed for gorse control have performed unexpectedly well on legume species that have been domesticated for human or farm use (Hill and O'Donnell, 1991; Hill *et al.,* 1995; R. L. Hill and A. H. Gourlay, unpublished data). This partial utilization of nonhosts may be the result of the loss of oviposition or feeding inhibition characteristics from the plants in the course of plant breeding for agronomic purposes, rather than a measure of host acceptability (Hill, 2000).

Tests were conducted with females that had already fed on gorse, and the few eggs laid on test plants may have matured during this preoviposition period (Schwarzlaender *et al.,* 1996). Although larvae could not complete development, adult thrips survived for significant periods on otherwise unfavorable hosts, maintained by minimal feeding. Thrips even survived for several weeks in damp petri dishes without plant material at all. This ability to survive led to exploratory feeding on nonhosts, but this was barely observable. It is therefore possible that *S. staphylinus* will be found as vagrants on nontarget plants in the field, as literature records suggest, but our experiments also suggest that it is unlikely to cause significant damage to those plants.

S. staphylinus was released in relatively large numbers at all sites and established with ease in a wide range of climates in both New Zealand and Hawaii. This confirms recent findings by Memmott *et al.* (1998) that founding populations of 270 *S. staphylinus* had greater than 80% probability of establishment, and that probability approached 100% when 810 thrips were released. The ability of adults to survive without significant feeding is a powerful adaptation that must enhance the ability of flightless adults to disperse by walking or jumping. Thrips have not spread far from release points in New Zealand. The mode of dispersal is not clear, but a high proportion of brachyptery in adults may be a barrier to short-distance dispersal. It is interesting to note that thrips of United Kingdom origin dispersed poorly in both Hawaii and New Zealand, whereas thrips from Portugal appeared to spread rapidly in Hawaii.

Thrips are serious pests of crop plants worldwide (Lewis, 1973). Host-specific thrips clearly have potential as biological control agents for weeds, but have been used only three times before. *Liothrips urichi* Karny has been used against *Clidemia hirta* L. in the Pacific, *Liothrips mikaniae* (Priesner) against *Mikania micrantha* Kunth in Malaysia and the Solomon Islands, and *Amynothrips andersoni* O'Neill against *Alternanthera philoxeroides* (Mar-

tius) Grisebach in the United States (Julien and Griffiths, 1998). *S. staphylinus* has been established in New Zealand and Hawaii for over 6 years. Discernible bronzing of gorse plants, but not plant death, has been observed in the field, and it is not yet clear how much this species will contribute to the biological control of gorse. Laboratory studies suggest that *S. staphylinus* can significantly affect gorse, especially seedlings. In the only published study of the impact of *S. staphylinus* on gorse, low numbers of adult thrips reduced growth of small plants in the laboratory after only 3–4 weeks (Fowler and Griffin, 1995). Other studies on the impact of thrips on gorse seedlings confirm this observation (P. McGregor and P. Peterson, Landcare Research, New Zealand, unpublished data), but there has been no research into seedling colonization behavior in the field. Populations of *S. staphylinus* increase rapidly in the laboratory and usually kill 2- to 3-year-old potted gorse plants within two to three generations, making the maintenance of thrips cultures difficult (R. L. Hill, personal observations). Such large natural populations have not been observed in the field in the United Kingdom and have not yet been recorded in New Zealand or Hawaii.

The factors that regulate the population density of *S. staphylinus* in Europe are not known. Possible natural enemies include Anthocoridae, predatory thrips, and spiders. The particular species of these natural enemies that prey on *S. staphylinus* on gorse in the United Kingdom will, in most cases, be absent from New Zealand, but other related predatory species may have some impact on introduced *S. staphylinus.* However, it is probable that the overall mortality caused by natural enemies on the thrips will be less than that in the United Kingdom. If so, we might anticipate higher levels of population density of *S. staphylinus* on gorse in New Zealand than in Europe.

There is no evidence that *S. staphylinus* can kill mature gorse plants. However, the classic study by Waloff and Richards (1977) indicated that the herbivores of Scotch broom (*C. scoparius*) reduced the longevity of plants by as much as 50%. Rees and Paynter (1997) presented evidence that broom plants live longer in Australia than in Europe and suggested that the lack of specialist herbivorous insects may be the reason for the increased lifespan of broom. If so, it follows that the establishment of specialist biological control agents such as *S. staphylinus* or the other four foliage-feeding insects introduced to New Zealand (Harman *et al.,* 1996) may significantly influence gorse population dynamics, even if the impact on individual plants is not lethal. Fowler and Griffin (1995) have shown that the cumulative effects of such control agents may be greater than those of any agent alone.

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